

The Human Co-operation Syndrome

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1. Introduction

The differences between humans and our close living relatives are so profound, and have emerged so rapidly, that it is probably a mistake to look for a single key adaptation; the single crucial change foundational to all the others. A more plausible model pictures our evolution in terms of a positive feedback links between a set of correlated changes; we evolved via coevolutionary interactions amongst a suite of cognitive, behavioural and social capacities. One of these is our capacity to co-operate. Human co-operation is a distinctive feature of human lifeways. It is one respect in which we contrast profoundly with the surviving great apes and (through its connection with information pooling, and the expansion of technology and of complex co-ordination) it is intimately connected with the crucial cognitive capacities that distinguish us from our living relatives: language, theory of mind, causal reasoning. So to understand human evolution, we must understand how this co-operation suite was assembled.

Human co-operation is itself a syndrome that involves at least the following three elements. (i) Human social life depends on information pooling and social learning. We are obligate, habitual, inveterate and adapted social information pumps, sucking information and expertise from our social partners (and, of course, occasional misinformation as an inevitable side-effect). Human life depends on this informational commons. For we have long depended on technology and technique to extract resources from our environment, and we acquire the technique, and the information needed to wield the technology, socially. Foragers do not invents the technology, the technique and the lore needed to extract resources from a recalcitrant world themselves. They may improve on the informational resources they inherit, or fine-tune those resources for their specific circumstances, but they inherit their essential cognitive capital. Moreover, human children have long childhoods: they have plenty of time to absorb the accumulated information and skills of their parent's generation, before their time budget is blown by having to earn their own living.

This picture of the importance of cross-generational information flow is not an artefact of western cultures. Explicit teaching may be more central to contemporary

western culture than to most others, but social worlds can be engineered to ensure cross-generation flow without explicit teaching, as is illustrated in a recent survey of the role of learning in forager culture (MacDonald 2007). This survey indicates that there is relatively little explicit stand-alone instruction, but there is a good deal of question answering; a rich body of narrative lore¹. So linguistically coded information is important in the learning process, even though little is explicit teaching. There is also a lot of informationally rich participation in adult activities, both in foraging and in artisanship (children begin to acquire tradecraft by helping their parents). Such adult activities are sometimes reorganised to make them safer or more informationally valuable to children: hunting parties leave in the day rather than in darkness; allow questions rather than hunting in silence; they choose territories and targets that make it possible for children to come with them. Material culture also helps: many forager villages keep a large range of semi-wild pets; children are provided with toy hunting weapons; many games practice crucial physical skills. The general picture that emerges is that there is lots of structured trial and error learning (children begin to learn about hunting by accompanying parents/other male relatives); lots of practice guided by observation learning; some but relatively little explicit teaching but lots of lore: the narrative life of the community is an important data source. In brief, crucial skills are acquired through hybrid learning coupled with downstream niche construction.

On the “embodied capital” model of Robson, Hill, Gurven and Kaplan, this flow of information across the generations is so important that human life history has shifted to accommodate it (see for example: (Hill and Kaplan 1999; Kaplan, Hill et al. 2000; Robson and Kaplan 2003; Gurven 2004; Kaplan, Gurven et al. 2005)). While I think they are right, this suggestion remains controversial. No-one doubts that foraging is a skilled activity, or that young foragers learn a good deal from their parental generation. But there is a good deal of scepticism about the idea that extended juvenile dependence is an adaptation to the informational demands of foraging. The sceptical idea is that humans are especially equipped for fast, accurate and high volume social learning, and that the observed covariation between forager success rates and age is a signal of the importance of growing size and strength rather than

¹ (Gurven, Kaplan et al. 2006) emphasise this too, in discussing the Tsimane, (p467)

20+ years of social learning (Bird and Bird 2002; Blurton Jones and Marlowe 2002). Children complete learning before they complete growing. Attempts to settle this question empirically have not been convincing. There has been experimental tests on the importance of learning time on a few important forager skills in a few cultures, and some attempt to measure success rate while controlling for motivation and other extraneous factors. But the attempts to measure skill all focus on the use of technology rather than its production. And the naturalistic method of measuring success in the wild treats individual success as a reflection of individual competence (Bock 2005; Gurven, Kaplan et al. 2006; MacDonald 2007). But it may well be the case that individual foraging activity is in part the result of both consultation with, and advice from, others. In measuring individual success, it is not at all obvious that we can idealise away from social inputs. So the data are meagre, ambiguous and narrowly based. There seems to be some signal of the importance of deep experience, but it is far from conclusive.

Still, even if it does not take 20 years to acquire foraging expertise, that expertise depends on extensive social learning. In this adult structuring of children's worlds, we see the intimate links between the evolution of co-operation and communication. Communication is a co-operation problem. Information is a resource like any other, so individuals with divergent interests will be tempted to take and not give. Moreover, sensitivity to the signals of others risks deceptive manipulation by that agent (Krebs and Dawkins 1984). But even if there is no problem of free-riding, we still need to explain the profit of co-operation (Calcott 2008). In thinking about this problem, Dan Dennett points out that an information gradient across a social world creates a potential profit from communication. Communication is mutually beneficial when different agents have access to different portions of their group's total informational resources (Dennett 1983). As he points out, such an information gradient is a side-effect of the fission-fusion foraging style of chimps, bonobos and (presumably) early hominins: these agents do not forage in a single convoy, so they experience differing spatio-temporal patches of their home range (Dennett 1988).

These information gradients were steepened in human social worlds by the role of experience in subsistence activities and by increased life expectancy itself (all

intensifying an intergenerational gradient). They are also steepened by sexual and other forms of the division of labour; in general, by specialisation. These steeper gradients amplify the potential profits of communication, thus stabilising the positive feedbacks between co-operation, communication and technical intelligence. Obviously human communication is not always frank and honest. We lie and conceal. But to a striking degree, human communication is co-operative: we do not always have to flitch expertise from others, nor wait for it to be manifest in the workaday lives of those with it. Teaching may not be ubiquitous. But we are often deliberate and expert teachers; the knowledgeable sometimes deliberately structure the flow of information to the ignorant in ways that enhance their access to crucial expertise.

(ii) Our informational commons is coupled to economic and ecological co-operation. Obviously, economic life in all large scale contemporary societies (indeed, in all mass societies) depends on collective action: in our social world, there are many essential tasks which cannot be completed by a single individual acting alone. So modern life depends on collective action, co-ordination and a division of labour. But there is persuasive evidence that collective economic action and a division of labour is an ancient feature of hominin lifeways. Meat consumption became a key part of hominin diets, probably via increasingly aggressive scavenging as a precursor to actual hunting, and it did so long before there is evidence of high velocity projectile weapons. If the impressive Pleistocene predators were dispossessed of their kills by volleys of thrown “handaxes” and/or stone-tipped javelins, we can safely assume that this was not a solitary (or even a small group) activity. Humans evolved a distinctive foraging style: it was information-rich, co-operative, tool-assisted, and it targeted high value resources (Sterelny 2007). Both *sapiens* and Neanderthals depended on animal resources that could only have been captured by bands acting co-operatively, and that suggests that collective foraging dates back at least to the last common ancestor of the two most recent hominin species. Both species have been successfully hunting large game for hundreds of thousands of years². But without the ability to kill at a distance, large game can be taken only by groups acting together.

² See for example (Jones 2007) for a vivid account of the collective consumption of a horse kill site at Boxgrove, England, dated to about 500,000 bp.

(iii) Humans co-operate reproductively, not just economically. Human life history evolution has resulted in long periods of total or partial dependence of children on their adult protectors. Though children forage in many traditional communities, in very few do young adolescents gather all the resources they need (still less even younger children). So intergenerational resource transfer are a persisting and entrenched feature of human life, as children throw a long resource shadow over their mother's future; (Hrdy 2005) estimates that it takes 13 million calories to raise children from birth through to full independence (pp 15-16). Yet human mothers wean their children early, on average between 2 and 3. Chimps wean at about 5 years; orang-utans even later (Kennedy 2005). But again in contrast to these great apes, human fathers invest in their children, providing some mix of protection, resources and direct care. Older siblings also often contribute to the family economy, again through some mix of provisioning and direct care of young siblings. But according to the Kristin Hawkes, Nick Blurton Jones and Frank O'Connell, the most distinctive element in reproductive co-operation is the role of grandmothers (Hawkes 1994; Hawkes, O'Connell et al. 1998; O'Connell, Hawkes et al. 1999; Hawkes 2003). Menopause is a very unusual feature of human life history: many women live for many years as active and competent agents after the birth of their final child, and these active grandmothers often play an important role in the care of their grandchildren. Chimp populations do not have this demographic profile. Chimps do not live as long as people, and female chimps do not have long and active post reproductive lives. Hawkes, Blurton Jones and O'Connell argue that this feature of human demography is not just distinctive, it is critical. Reproductive co-operation was the foundational form of human co-operation, and grandmothereing was the critical adaptive breakthrough in the evolution of the distinctive form of human reproductive co-operation.

For Hawkes, Blurton Jones and O'Connell the pivotal member of the hominin lineage is *H erectus*. For while the evolutionary changes that resulted in modern humans took place gradually and over a long period, one can see *erectus* evolution as the time hominins became human. For *erectus* was the first of the out-of-Africa hominins; the first species in our lineage to expand geographically and ecologically. Its anatomy became human: *erectus* hominins were our size; fully bipedal; large-brained (though

not as large as ours); sexually dimorphic to a similar degree. Perhaps they also evolved towards *sapiens* life history patterns, with a lengthened lifespan and a longer period of juvenile dependence. Hawkes, Blurton Jones and O'Connell take as their point of departure these life history patterns. In comparison with chimps (and our presumptive common ancestor), we are longer-lived, larger, and our children are dependent much longer. In the recent past, a hunting hypothesis related the *erectus* geographic and ecological expansion to the evolution of collaborative hunting and central place foraging. Humans consumed the proceeds of hunting in groups, in domestic circumstances not too dissimilar to those experienced by recent foraging cultures. The cognitive demands on this ecological style selected for lengthened juvenile dependence, to give children the time to acquire the information and skills they would need as adults. This explanation of our life history evolution depends on a model that is very specific to humans. The grandmother hypothesis, in contrast, relies on Charnov's general model of life history evolution while at the same time developing a sceptical re-analysis of the role of hunting in human evolution. Hunting, the sceptics argue, is male display rather than family economics; mating effort rather than breeding effort.

2. The Grandmother Hypothesis

Charnov's general model of life history evolution begins with the idea that when all else is equal in K-selected environments, selection will favour larger body size (and hence delayed sexual maturity). In such environments, fertility rates are low, and parents invest heavily in the relatively few offspring they produce. Thus size and strength is an important factor in many competitive interactions. But typically, all else is not equal. Size has to be paid for by delaying maturity, and delay is inherently risky. If the parents are at high risk of dying before their offspring are independent, or if the offspring are themselves vulnerable, that risk is too great. For many animals, the adult survival rate is too low to allow organisms to risk long juvenile periods and a slow growth to adulthood. They are likely to die before they recoup their investment in growth. But if there is an decrease in mortality rates, and risk falls, organisms can invest in size, delaying maturity. If the risk of sudden death is lowered, it is also worth investing in anti-aging physiology. For the rate at which animals senesce is itself

variable and responses to metabolic investment. So we should expect to see positive correlations between long lifespans; large body size; delayed sexual maturity..

Hominins fit this basic pattern: we are primates with long lifespans, delayed maturity, and large body sizes. However, we contrast with other large-bodied long-lived primates (and mammals) in that females often have a long, active & healthy post-reproductive life. Women abandon direct reproductive effort, often long before they die. Why? According the Grandmother hypothesis, active post-reproductive women are an evolved response of the *erectus* lineage to the decreased risk of adult mortality in increasingly seasonal environments. The reduction in mortality indirectly extended time as a juvenile via selection for increased adult size and thus delayed maturation. So children stayed children longer. Yet they needed more care, for in dry seasons children could not gather their own resources. As intensified climatic variation increased the seasonality of *erectus* environments, the hominin lineage faced a choice. Find dry-season resources and a way of delivering them to the young, or retreat to less seasonal refuges.

Washburn's hunting hypothesis was one candidate solution to this dilemma: meat and marrow are available in the dry season, and adult males (especially) deliver these resources to women and children in (extended) family units ((Washburn and Lancaster 1968); for a more recent version of the idea, see (Stanford 1999). Hawkes, Blurton Jones and O'Connell have another suggestion: underground storage organs (USOs) are the dry season resource, and (in fortunate families) active grandmothers find and deliver these resources to the older children of her daughters. This allows those daughters to care for their infants, thus reducing the interbirth interval of families with active grandmothers. Selection would thus favour both a late-in-life switch of female strategy from direct reproductive effort (presumably because its prospects for success, even of an active grandmother were low) and investment in anti-aging physiology³. The idea is that fairly modest periods as an aiding

³ There seems to be alternatives to menopause and grandmothereing. Another strategy would require the evolution of facultative variation in developmental schedules of late birth children: one involving accelerated puberty and sexual maturity for late-birth children. There is some evidence that puberty/sexual maturity can be facultatively

grandmother would be visible to selection, so active grandmaternal life could evolve (once extrinsic risk declines) by degrees. To improve her direct fitness, a potential grandmother going it alone as a late-life mother would have to survive as a competent agent through the whole period of the dependence of her final child. To improve her indirect fitness she might need only to take care of one three year old through one dry season, thus enabling her daughter to squeeze an extra infant into her lifetime fertility schedule.

In short, the grandmother model has five key components. It requires (i) a reduction of extrinsic mortality; this made delaying maturity profitable and opened the door to profitable investment in slowing senescence. (ii) That reduction in mortality took place in environments which were increasingly seasonal, hence weanlings could not support themselves year-around by their own foraging. (iii) In dry season environments, late-mature women could generate a nutritional surplus; they could feed both themselves and a daughter's dependent child. (iv) The social organization was not philopatric, with males staying in their natal group, and females leaving. For the model to work, mothers must live in the same group as their reproductively active daughters⁴. Moreover, they must be able to recognise their grandchildren. The recognition requirement is not trivial. For some fraction of mothers would have sons as their only adult children, and there are many breeding systems in which males cannot track their offspring. Since Hawkes, Blurton Jones and O'Connell are sceptical about the idea that males provision by hunting, it is not surprising that they formulate the Grandmother Hypothesis as an idea about mother-daughter reproductive alliances. But this does exacerbate a potential problem for their model: were there enough grandmothers with living, reproducing daughters for selection for grandmothing to alter human life history? So the model also requires: (v) Hominin populations contained a reasonable proportion of older adults: the strategy of abandoning terminal direct breeding effort in favour of grandparenting can invade in

tuned, so it would be interesting to know whether this is a road partially trodden; whether late children are smaller and faster-maturing (and perhaps female-biased)).

⁴ This residential assumption is probably reasonable, (Hrdy 2005) argues that great ape residential patterns are adaptively plastic, so if younger women did better by staying at home, they would stay at home.

reasonable numbers, making the linked behavioural and physiological dispositions visible to selection.

How reasonable are these assumptions? I shall argue that a modest version of the grandmother hypothesis is plausible; namely: that grandparent-based reproductive co-operation was one part of the co-operation revolution in human life. But I am sceptical of the more ambitious idea that the evolution of the nurturing grandmother was the key innovation — the adaptive breakthrough that drove the hominin transformation. So I aim to synthesise reproductive co-operation with a more traditional, ecological, model of the co-operation revolution, but in the context of a model which emphasises the general role of niche construction and cultural inheritance in human evolution.

Hawkes, Blurton Jones and O’Connell themselves are most concerned to defend the demographic assumption: that there actually were grandmothers in ancestral populations in reasonable numbers. It is often suggested that long life expectancies are the privilege of modern populations: populations of humans in traditional societies, and even more still more ancient populations, rarely contained the old in significant numbers. Not so, according to Hawkes, Blurton Jones and O’Connell. They argue that there is independent evidence that long human life spans have a deep history. Ethnographic evidence of foraging peoples shows that such populations include significant numbers of post-reproductive adults (often about 20% of the adult population is over 45). Moreover paleodemographic claims that ancient populations lack old survivors are undermined by preservation biases: these paleodemographic views depend on skeleton assemblages, and older folks’ bones are less likely to survive than younger ones. So they suggest that the basic pattern of *sapiens* seems to be essentially stable over forager-agriculture-urbanisation transition, despite real changes in fertility and life expectancy. Populations may contain post-reproductive adults as a significant fraction of the population, even if average life expectancy is in the 30s or early 40s. For such averages are compressed by large numbers of early deaths. So even if at-birth life expectancy approximates 40, helpful grandparenting will be visible to selection.

Gail Kennedy has argued the contrary view, suggesting that the grandmother hypothesis is demographically implausible because of very heavy early adult mortality (Kennedy 2003; Kennedy 2005). There were simply not enough late-reproductive women for selection on grandmothing skills to have evolutionary consequences. But the direct palaeodemographic evidence she develops for this claim is unconvincing. Even if preservational biases can be discounted, for early *homo* the sample sizes are too small, and may not be representative. That said, in most of the samples she cites, there were significant percentages of older adults⁵. Moreover, Kennedy's own model of life history evolution fits poorly with the claim that ancient hominin populations had few mature (let alone aged) adults. For she agrees that that human life history evolution extended the period of juvenile dependence. As hominins evolved, the period of dependency increased. It is very hard to reconcile this model of life history change with the idea that those very populations sustained heavy death rates in the 20s and early 30s. For this would imply that many children and young adolescents would lose their mother while still dependent. As is known from populations under serious hunting pressure, elevated death rates amongst primate adults in a population selects for accelerating sexual maturity, not extending juvenile dependence.

To reconcile her palaeodemography with human life history evolution, Kennedy is forced to posit high rates of allomothering. But this scenario is implausible. While ancient primate emotional responses may prime hominin allomothering (Hrdy 2005), there will be selection for those responses only if the costs are low for allomothers and the benefits are high for infants and mothers. Protection and babysitting may well fit this cost/benefit structure. Low-cost protection can release the mother to forage for herself and her young. Sibs and even more distant relatives might well reap inclusive fitness benefits by occasional child guarding. The cost/benefit picture changes dramatically if it is supposed that allomothers forage for another's young on a sustained basis. It is one thing to suppose allomothering might have anciently supplemented maternal care; another to suppose it could have regularly replaced it.

In short, the demographic foundations of the model are credible, though we lack much direct evidence of the age structure of pre-sapiens populations. Likewise, the idea that reproductive co-operation is a central component of human co-operation is plausible. In many cultures, mothers have shorter interbirth intervals than chimps, even though humans are subadults for much longer, and even though weaned human children, but

⁵ So her table 1, on p 555, in all samples of over 100, more than 10% were of older adults, of 40+ years (Kennedy 2003).

not weaned chimps, need not just food but a host of other resources too. These include shelter, clothes, protection, social support and education — we should not forget the costs of informationally engineering children's learning environments. *Erectus* children would have required some of these extra resources too. Higher cost children plus shortened interbirth intervals signals reproductive co-operation.

That said, I have two crucial reservations about the ambitious version of the Grandmother Hypothesis. Reproductive co-operation is only one element of the co-operation suite. Moreover, there is good reason to suppose that these evolved in concert: reproductive co-operation did not evolve first, forging a platform for other forms of co-operation. Second, grandmothing was probably only one element of reproductive co-operation. Older siblings, aunts, and even fathers and paternal relatives are often important in *sapiens* social worlds. There is no reason to suppose that these alternative channels of alloparental support have more recent origins than grandmothing. The extension of subadult life made older siblings available as potential sources of protection, education and support for longer. Moreover, siblings are as closely related to one another as mothers are to their children, so an aging female abandoning direct reproduction can gather as much indirect fitness benefit as an aunt as she can as a grandmother. That was especially true of mothers with only sons, so auntying is as likely as grandmothing. And while I accept that in ancient hominin social worlds, many mothers would still have had their own mother alive, many would not. As Hrdy points out, even on optimistic assessments of survival, only about 50% of mothers would still have their own mother; on other estimates that falls to about 25% ((Hrdy 2005) p16). If allomothing was virtually essential for successful reproduction by earlier hominins, there must have been much allomothing that was not from the grandmother.

Finally, what of fathers? Hawkes, Blurton Jones and O'Connell are sceptical about the importance of fathers as allomothers, because they are sceptical about the idea that hunting is a provisioning tool. I dissent from their view of hunting in some detail in section 4. But let me begin with a telling point from Gail Kennedy. She points out that growing children need very specific resources. Weaned young children need more than calories: they need protein to fuel their post-birth brain growth. Hawkes, Blurton Jones and O'Connell finger underground storage organs as the key resource provided

by grandmothers, but scavenged brains and bone marrow are the most plausible source of these protein needs, and such scavenging is unlikely to be a grandmaternal speciality.

The early age of human weaning has serious costs: weanlings have a higher exposure to pathogens at an age where their immune system is less well-developed, and when they lose the indirect immunological benefits of mothers' milk. The Grandmother Hypothesis assigns the benefits of early weaning to mothers: early weaning, supported by allomothering, reduces the interbirth interval and increases lifetime fertility. Kennedy thinks the compensating benefits derive from the child's need to fuel post-birth brain growth, given the unsuitability of maternal milk to fuel that growth once children are roughly of weaning age. So the benefits accrue to infants: they avoid the protein gap (driven by brain growth) that would open out as protein needs increase beyond the point that they can be sustained by maternal milk (Kennedy 2005). If this nutritional argument is sound, there may well be an important link between the establishment of lithic technologies, large carcass exploitation through scavenging and bone-breaking (very likely in the face of competition from other scavengers and predators) and the evolution of childhood as a stage of hominin life history. So first suggested modification of the Grandmother Hypothesis: think of grandmothers as just one element of the evolution of reproductive co-operation.

Moreover, there are tacit features of the model that imply that the evolution of grandmothers took place in a social environment that was already co-operative. The model assumes that the social environment is benign. Most USOs cannot be consumed on the spot; they need to be processed. Moreover, they are often quite sizable packages of food. In a Hobbsian social world, grandmothers and infants with such resources would often lose them, and not just to occasional unfortunate encounters with the largest males. They would be vulnerable to junior and subadult males as well. In such social environments, the vulnerable need to adopt a feed-as-you-go foraging style, and USO harvesting and processing would not be viable. So the social environment must have been at worst passively co-operative. Furthermore, Charnov's basic life history model connects the extension of the human lifespan to reductions in extrinsic mortality. This reduction was not the result of a more benign external environment. To the contrary, Rick Potts argued that the frequency and magnitude of environmental fluctuations increased in the second half of the human career (Potts 1996). While Hawkes, Blurton Jones and O'Connell are silent on the

reasons for the fall in mortality, the most plausible suggestion is that increasing co-operation reduced risk, by more effective defence against predation, and by dampening variance in food supply. Social support through illness and injury might also have been important. Very basic nursing — providing food, water and protection — greatly improves the survivability of serious injury and illness. Finally, USOs — the key grandmother resource — are rich. But finding them can be challenging and more crucially, as I have just noted, they often require complex cultural adaptations to process. Many are inedible without cooking, or washing and leaching to remove toxins. Yet building complex adaptations is a signature of information pooling and social learning; one of the crucial elements of the co-operation syndrome described in section 1. Grandmothering evolved in a milieu of other forms of co-operation; both reproductive, informational and ecological. It was part of an evolving co-operation suite; perhaps not even an especially central element in that suite.

3. Foragers: Ancient and Modern

On one model of life history evolution, human life histories have been structured by the demands on social learning. Adult life is delayed, and cross-generational resource flows organised because the adult high-expertise foraging mode is very profitable. Adult foragers, especially males, deliver a lot of resources. But the expertise necessary to generate this profit takes many years to acquire. Childhood is an adaptation to the extensive demands of social learning; it can be afforded only because that learning makes adult activity far more profitable than it would otherwise be. This view of human life history takes hunting to be centrally an economic activity. It is provisioning rather than signalling. The costs of learning are worth paying, because adult provisioning, especially adult male provisioning, is much more profitable as a result of this investment. So there is a link between models of the sexual division of labour and of human life history. Thus those who think of hunting as primarily economic think of lengthened juvenile periods as adaptations for the accumulation of expertise. Those sceptical of this view of hunting, think of long childhood as a side-effect of the extension of adult life, and of the selection for increased adult body size.

While there has been many attempts to use paleoanthropological data directly to settle these evolutionary questions, in thinking about ancient foragers, modern models loom

large (O'Connell 2006). They have been important as a lens through which to interpret the remains of ancient lives. This poses a *prima facie* methodological problem, for there are profound differences between ancient and modern foragers. But despite those differences, there are some questions about ancient lives to which modern data is relevant. In considering the cognitive co-operating foraging model of human life history, modern data offer a conservative test. The ancient to modern transition would tend to damp down the critical features of ancient forager's lifeways; i.e. it would damp down those features identified as critical by the collaborative foraging model of human lifeways. So if we still find those features in modern foragers, we can reasonably project them back onto the lives of ancient foragers.

Foragers and their world have been transformed over the last 150,000 years (for a good review, see (Stiner 2002)). One important transformation has been in the environment of co-operation. Maintaining stable co-operation has become more problematic. In my 2007, I argued that humans extract resources from their environment in a unique way: via collaborative expertise. Foraging is both co-operative, and dependent on expertise and technology (Sterelny 2007). Over the last 40, 000 years, the pattern of collaborative foraging has changed markedly. The broad spectrum revolution (BSR) involved, *inter alia*, a shift away from large and medium size game (ancient *sapiens* specialised in ungulates) to small and medium size game, and to marine and other resources (Stiner 2001). The BSR selected for specialisation (as different techniques and technology are needed for hunting, say, rabbits rather than wildfowl or fish) and for much more small group and individual hunting. At the same time, this shift reduced both variance in daily success and average package size. Kills were much more frequent, but much less was provided per kill. So in many environments, hunting became less collaborative, and the need for reciprocal sharing less pressing.

This social effect of the BST was intensified by the projectile revolution. For perhaps the first 200,000 years of hunting and bully-scavenging, tool kits were simple and weapons fairly short-range. (A thrown, stone-tipped spear is unlikely to have a kill zone much beyond 10 meters). If humans between 200,000 and 40,000 had regular access to the meat of large animals, either by direct kills and by expropriating the kills of other large carnivores, technique and co-operation must have been crucial.

Between (perhaps) 30,000 bp and 20,000 bp, humans added spear throwers, bow & arrow, and poison darts to their arsenal (Marlowe 2005). This changes the environment of co-operation. It became possible for individuals or small groups to kill large animals in relative safety. Large groups that hunt and kill together can share on the spot. There may still be a problem in controlling a greedy bully who wants to take more than his share, but because the profit of joint activity is accrued together and in full view of all, there are no informational problems in policing co-operation. What counts as fair is less problematic, if everyone is a roughly equal partner in a joint activity. The same is not true once individual success become highly variable (as individuals hunt alone or with favoured partners); once the range of resources expands (making commensurability an issue); once reciprocation extends over time; and once individuals spend much of their time, and enjoy much of their success and failure, away from the eyes of the many. Co-operation, all else equal, is most stable in small, homogenous groups. There is little robust evidence on group size over the last few hundred thousand years, though its usually supposed to have increased (Dunbar 2003). There is more robust evidence of increasing heterogeneity and role differentiation, exacerbating the cognitive challenge of monitoring fairness. I conjecture that co-operation became more fragile, and that the developing archaeological signature of ritual and public symbol use over the last 100, 000 years is a response to this fragility.

There has also been a transformation in the cognitive demands on a forager's life. In some respects, those may well have increased through the BSR and the expansion of material culture. For instead of having to have a detailed understanding of a few key target species, after the BSR foragers had to have a feel for the natural history of many. Instead of having to master the techniques of producing a limited toolkit, they had to master the production of a much more varied technology. In other respects, the cognitive demands are less onerous (especially if the production of physical symbols allowed them to store information in the world). The use of dogs reduces the pressure on tracking skills; of projectile technology on concealment and stalking⁶. Crucially,

⁶ The dates of dog domestication are unclear. The fossil evidence suggests that canine domestication was relatively recent, and Australian aboriginals did not have domestic dogs. Perhaps about 12,000 years ago. But molecular evidence suggests a much deeper date, of around 120,000 years (see (Pennisi 2002)).

though, many (perhaps all) foraging peoples have now supplemented or replaced home-built technology with store-bought equipment. As a consequence, empirical measurements of the importance of learning all focus on foraging itself, rather than the cognitive demands of being equipped to forage. At best they measure only one aspect of the skill set of ancient foragers.

Finally, the economics of hunting have changed, dampening down the differences between male and female activities. The BSR has made much male hunting (that targeted on small game) more like gathering: less variance; less physical risk; it has become more of an individual activity, with less communally shared; and very likely with a lower rate of return per hour of effort. For the BSR is supposedly driven by foragers being forced to seek increasingly less rewarding targets, as encounter rates with the more desirable targets fall. With the massive depletion in most habitats of large-medium to large herbivores, hunting by contemporary and near-contemporary foragers is probably much less profitable. They live in a more Malthusian environment: the human footprint on the local resource profile has been heavy, persistent, depleting. Hunttable resources are less abundant, and those that remain are targeted by more.

Somewhat paradoxically, it is possible that women's and children's foraging is more valuable. The idea that an extended childhood is an investment paid for by increased productivity as an adult supposes that children and young adolescents have to be supported while their expertise develops. For while it is true that in favourable circumstances, children can contribute significantly to the family economy, in very few environments are children fully self-sufficient before their mid-teens. In most environments there is seasonal variation, so there will be parts of the year when resources are hard to extract. Moreover, children's contribution to the family economy often depend on technology which adults provide. Even now then, children are not self-sufficient. The difference between modern and ancient children, though, is that in many environments children's semi-independent foraging is possible only because predators have been largely eliminated, and those that survive have learned to avoid humans. This is probably a relatively recent, Holocene development, one that

has eased the energetic demands of children on their parents. To a lesser extent, the same may be true of female gathering: if we set aside the threat from other humans, this is surely much safer than it was 100,000 years ago, when we were one of an impressive set of African Pleistocene predators.

Thus contemporary and ancient foragers did not face similar ecological, social and sexual decisions with similar resources. Ancient hunting was probably more routinely co-operative, with large kills shared on the spot amongst quite large hunting parties. The most available prey was more abundant both relatively and absolutely, and so the profit of hunting was probably higher. Gathering by women and children may well have been somewhat constrained by predation threat. Ancient hunters had to manufacture all their own equipment; detect and get close to their prey; track prey with their own observational powers rather than piggyback on those of dogs. So if the results of hunts are still regularly shared; if hunting is more profitable to hunters and their family than gathering; if foraging in general and hunting in particular is highly skilled, where size is not everything and older and more experienced hunters still do better than young adults in their physical prime, then we can extrapolate these traits and then some to ancient foragers.

4. Hunting: Provisioning or Signalling?

Hawkes, Blurton Jones and O'Connell do not think of hunting as primarily a provisioning activity; in particular, large game hunting functions to send a costly signal: hunters advertise their quality. The crucial idea of costly signalling models is that agents have an interest in advertising their high quality (typically to potential mates), but that less fit agents have an interest in overstating their quality. Costly signals enable the audience to discriminate between high quality agents and pretenders, because the signals are not just costly; they are differentially costly. Frauds cannot afford the signal, and so its reliability is stabilised by the differential cost of sending it (Saunders forthcoming). Hunting, the idea goes, is an unfakable signal of quality: only the genuinely fit hunt successfully (Hawkes 1991; Hawkes and Bird 2002; Smith and Bliege Bird 2005). Despite its popularity, I think this model is quite unpersuasive. We should expect costly signalling to be an individualistic

activity: as is, for example, building a new art gallery for a city. But this does not fit the pattern of hunting in many forager societies. Hunting is often collective and co-operative rather than individual (see for example (Alvard and Nolin 2002) on co-operative whale hunting). Indeed, as I argued in section 3, only the invention penetrating projectile weapons made individual and small group large game hunting possible. Such technology is very recent: a recent table lists spear-throwers as dated to 17,000 years ago; bows and poison to around 11,000 bp (Marlowe 2005) p64). Yet there is persuasive evidence that large game hunting played a central role in human economies long before these dates. So hunting became central to human life as a collective, co-operative activity.

We expect sending costly signals to be not just individualistic; it should be a minority activity. For the costly signal is a display of unusually high quality. So on the costly signal model, we would expect only the expert to hunt and share. Poor hunters should keep what they catch and scrounge what they can, or, more likely perhaps, they should abandon hunting altogether and forage like a girl. If hunting-and-sharing genuinely is individualist signalling for individual advantage, drop-outs need not fear being excluded from the distribution of product. They are not defecting from a co-operative activity: others should welcome their withdrawal from competitive signalling. Hunting should be like playing baseball in America: the best hunt, and the rest watch. But this does not fit forager ethnography: in many cultures, males are notoriously addicted to hunting. The hunting and sharing of the less expert remain unexplained.

Costly signalling is a natural model of some forms of prosocial behaviour in human life: bigman feasts; conspicuous gift-giving to charity; perhaps supererogatory displays of courage in inter-communal conflict (Smith, Bird et al. 2003). And there do seem to be examples of male hunting which fit the signalling paradigm. A persuasive example is that of Meriam turtle hunters. A crucial fact about the Meriam is that not all the males hunt (and few are hunt leaders). Moreover, Smith, Bird and Bird are able to show that turtle hunting does not make sense as an economic activity: there are alternative, and more rewarding sources of protein (and, in the right season, even of turtle meat). Successful catches are shared, with no evidence of family bias or

reciprocation. Finally, Smith and his co-authors are able to show that turtle hunters are fitter: they have a higher reproductive success, both because they acquire mates earlier than non-hunters and because they have higher-quality mates. (Smith, Bird et al. 2003). So while Smith and co cannot rule out the possibility that turtle hunting success and superior fitness have a common cause, the idea that turtle hunting is a successful and reliable signal of high quality is plausible⁷.

So some contemporary hunts probably are signals. But can we generalise from this example? The data is patchy and often qualitative, but the Meriam seem to emerge as the exception rather than the rule. First, Frank Marlowe argues if hunting is family provisioning, men will hunt less in those environments in which gathering is more profitable: namely highly productive tropical environments⁸. Marlow suggests that there is indeed evidence that men gather more in just those environments; so their hunting versus gathering decisions are sensitive to their rate of return; not what we expect if hunting is nothing but a costly signal of phenotype quality. Moreover, he also argues that male behaviour is too variable for hunting to be best seen as costly signalling rather than provisioning. For if the sexual division of labour is a family-level adaptation in response to constraints on female behaviour in the dual mother/forager role, male behaviours should be more variable than female behaviours, because male behaviour will be more sensitive to specific conditions and to female strategy. Female behaviour will be more rigid, because it is driven more by the invariant physiological constraints of pregnancy and lactation. So while it is sometimes good for males to gather, but it is rarely an option for females to hunt (though they do fish). This prediction seems supported by the data; male activity patterns vary more widely than those of females. For while the sexual division of labour is highly variable from culture to culture, it is also ubiquitous. Marlowe reports no culture in which men and women have the same pattern of ecological/economic

⁷ The more so, because Meriam women seem to likewise signal their fitness by collecting industriously and sharing generously. Gurven and Hill note that women share as much as men, when package size is held constant (Gurven and Hill 2006). They interpret that as a variance reduction strategy, but it can be fitted into a model in which each sex is under sexual selection.

⁸ It is also hard to reconcile the signalling model with the fact that in some high arctic cultures, there is almost no gatherable resources and families are dependent on male hunting.

activity (Marlowe 2007). But while Marlow's arguments are plausible, the data on which they rely are crude and surveyish.

Still, they are supported by other considerations. For while the Meriam turtle hunters do not seem to share with their group in expectation of reciprocation, nor use their catch to preferentially provision their families Gurven and Hill argue that this pattern of sharing is exceptional (Gurven and Hill 2006). They argue that hunters typically have considerable influence on the distribution of their hunting profits, and that these influences result in a bias towards kin (as a provisioning model would predict), and towards those that reciprocate. Food is given to those that give. Male sharing is either kin based or contingent. If Gurven and Hill turn out to be right that this is the general rule, then sharing large catches with nonkin is likely to be a variance reduction strategy. Moreover, hunting does seem to be a relatively efficient form of provisioning. While few studies are detailed and quantitative, several show that male hunting generates an average rate of return per hour of effort of around twice that of gathering. And calorie counts understate this difference: meat is much richer in reliable macronutrients (proteins and lipids) than vegetable based foods. But even if on average, hunting is no more productive than gathering, specialisation in different resources will generate synergies when the family unit has a variety of resource needs and when each resource can be gathered only by those with special skills and/or equipment⁹. Moreover, while it is true that returns for male hunting are more variable than those of gathering, it certainly does not follow from that that the economically rational, family-provisioning male would gather rather than hunt. For one thing, storage, sharing with other hunters, and female gathering all buffer variance. So to does hunting small game buffers variance, as small game is more reliably captured than large game. (Large animals are meat convoys; see (Hamilton 1971)). Finally, there is significant variance with gathered resources too.. In short, the transition from ancient to modern foraging is likely to have improved the fit of the signalling model with the data rather than eroded it. But even when we focus on contemporary foraging, the model fits the general trends rather poorly.

⁹ We do not need to suppose that women are constitutionally unable to hunt for the sexual division of labour to be stable: initially small symmetry-breaking differences followed by a positive feedback loop will do it.

5. Finale

On the Hawkes, Blurton Jones and O'Connell model of human evolution, increased seasonality is the key to the evolution of human co-operation. In so far as the evolution of human co-operation had an external, extrinsic trigger; that is, in so far as it was an evolutionary response to a change in the selective environment that occurred independently of human impact, I am inclined to agree. But that agreement comes with three caveats. First, I suspect that increased seasonality selected for ecological as well as reproductive co-operation. In particular, given that Pleistocene Africa boasted an impressive stock of predators; given that increased seasonality turned hominin habitat into savannah and woodland with much less natural cover than forest; and given that early hominins were not physically imposing, selection for effective response to predators would have been strong. So my best guess is that collective defence was an early and important element of the co-operation syndrome. Second, I think this process began (as did increasing seasonality) earlier than the evolution of *erectus*. The habilines used simple stone tools, and while the capacity to make and use stone tools may well not require high fidelity cultural transmission, it will have depended on some form of hybrid learning; perhaps socially primed trial and error learning. Some form of information pooling was beginning to characterise habiline life.

Finally, while the expansion of hominin co-operation may have required an initial extrinsic trigger, its origins altered the selective environment in ways that selected for further co-operation. The evolution of human co-operation was largely driven by positive feedback. I have conjectured that co-operative defence, perhaps using thrown stones (Bingham 2000) was an early form of hominin co-operation. Successful collective defence preadapts for further co-operation; in part by reducing mortality and selecting for the life history changes that make advanced social learning possible. But it also makes collective scavenging and access to predator's kill sites possible. Furthermore, it pre-adapts hominins psychologically and socially to the collective suppression of dominant, expropriating males, thus opening the door to collective foraging, central place foraging and (more generally) variance reducing strategies that rely on trust and secure possession of one's resources. On this picture; there is no key

adaptation or magic moment, Rather, human uniqueness depends on the evolution and stabilisation of a set of positive feedback loops which connect technology and the division of labour with co-operation, with social learning and with informationally engineered developmental environments. We are creatures of feedback.

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